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RECONSTRUCTING THEROPOD LUNG VENTILATION

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Although direct evidence concerning the lung structure of extinct vertebrates is not available in the fossil record, osteology and comparative anatomy provide an adequate basis for the reconstruction of ancient respiratory mechanisms. The shape and volume of the trunk put constraints on the overall lung shape, and the nature of rib-vertebra interlocking yields information concerning the mode of lung ventilation and the tidal volume. Additionally, osteology might contain evidence on various different aspects, like the existence of lung diverticula through pneumaticity of specific skeletal elements, or the presence of well-developed attachment areas for a diaphragm. When this information is properly complemented with the data that can be obtained by careful analysis of similar and different structures in phylogenetically closely related extant organisms, or similar structures in more distant extant fauna, quite often reasonable reconstructions of ancient respiratory systems can be constructed.

Theropods merit particular attention in light of their phylogenetic placement in between the Aves and other Archosauria. Birds are unique in having a lung with discrete groups of diverticula or air-sacs, which are instrumental in generating unidirectional airflow. The avian lung construction is technically much more efficient than the bidirectional airflow system employed in reptiles and mammals.

It is likely that the evolution of the avian lung must have occurred somewhere in the Theropoda-Aves lineage. Saurischian dinosaurs, like birds, possess pneumatic bones in specific positions in the skeleton. In theropods lung diverticula invaded the axial skeleton to varying extent. Skeletal pneumatization extends as far caudally as the sacral and caudal vertebrae in groups as the Oviraptorosauria and Tyrannosauridae. Theropods possess ribs with well-separated rib heads, defining specific planes of movement. Especially in more derived theropods distinct attachment areas for the intercostal muscles are present. Uncinate processes, which have been shown to increase the efficiency of costal breathing in birds, are present in theropods like *Velociraptor*. In addition, kinetic gastralia which are jointed in a characteristic interlocking pattern, are characteristic of theropods and also present in *Archaeopteryx*.

Considering the presence of dorsal diverticula, which invaded the axial skeleton, the lungs of theropods must have been attached dorsally. Heterogeneously partitioned lungs with extensive sac-like ventral and caudal regions were probably present. The ribs were adequately built for manipulation of the shape of the thorax. The gastralia prevented paradoxical movement of the viscera in the lung space upon inspiration. The exact extent of lung diverticula formation cannot be determined. If, however, the caudal sac-like lung region had differentiated to form abdominal air-sacs, the kinetic gastralia would have been well suited for ventilating them.

The morphology of the pelvis, the laterally flattened trunk and the extensive skeletal pneumatization in theropods makes the occurrence of a hepatic piston pump, analogous to the system employed in modern crocodilians, highly unlikely. Considering the similarities in the axial skeleton in advanced theropods such as dromaeosaurs and in *Archaeopteryx* and early birds, it is likely that unidirectional airflow became established relatively late in the theropod-avian transition. The prerequisites for cross-current gas exchange, however, are already present in the crocodilian lung.